

# A new view on migration processes between SIR centra: an account of the different dynamics of host and guest

Igor Sazonov<sup>a1</sup>, Mark Kelbert<sup>b</sup> and Michael B. Gravenor<sup>c</sup>

<sup>a</sup> College of Engineering, Swansea University, Singleton Park, SA2 8PP, U.K.

<sup>b</sup> Department of Mathematics, Swansea University

<sup>c</sup> Institute of Life Science, School of Medicine, Swansea University

## Abstract

We study an epidemic propagation between  $M$  population centra. The novelty of the model is in analyzing the migration of host (remaining in the same centre) and guest (migrated to another centre) populations separately. Even in the simplest case  $M = 2$ , this modification is justified because it gives a more realistic description of migration processes. This becomes evident in a purely migration model with vanishing epidemic parameters. It is important to account for a certain number of guest susceptible present in non-host centra because these susceptible may be infected and return to the host node as infectives. The flux of such infectives is not negligible and is comparable with the flux of host infectives migrated to other centra, because the return rate of a guest individual will, by nature, tend to be high. It is shown that taking account of both fluxes of infectives noticeably increases the speed of epidemic spread in a 1D lattice of identical SIR centra.

**Key words:** spatial epidemic models; migration dynamics; outbreak time

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## 1 Introduction

The classical SIR model is one of the simplest models which describes qualitatively a typical directly transmitted disease outbreak in a populated center, and remains the building block for many, more complicated applied epidemic models. The population is assumed to consist of three components: susceptible (S), infected (I) and removed (R).

Models of coupled epidemic centra are of particular interest because they describe epidemic spread through network of populated centra, and hence the overall population is not treated as a homogenous system. This is a subject of intensive research, we mention here just a few recent

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<sup>1</sup>Corresponding author. E-mail: i.sazonov@swansea.ac.uk

publication [2, 3, 4, 5, 6] not trying to provide an extensive bibliography. The old scenario, known from the middle ages, when the disease propagates locally from a village to the neighboring villages is replaced now by almost instantaneous propagation around the globe. This phenomena was analyzed in a many papers (see, e.g., [7, 8]). In particular, it was observed that on heterogeneous networks an increase in the movement of population may decrease the size of the epidemic at the steady state, although it increases the chances of outbreak. This motivates a detailed analysis of migration in inhomogeneous populations.

The coupling between nodes of such a network is mainly caused by migration processes of infectives. There are several models describing such coupling (see [9, 1]), for example, in [10] the influence of various parameters on the spacial and temporal spread of the disease is studied numerically, with particular focus on the role of quarantine in the form of travel restrictions. In [11, 12], the so-called diffusion like model is proposed and studied in the framework of a fast migration time approximation. Note that the model in [10] is a particular case of the diffusion model when the migration time tends to infinity but the coupling coefficient introduced in [11] tends to zero.

In all these models the guest population is completely mixed with the host one, so their dynamics is indistinguishable. Nevertheless, a more detailed consideration suggests that while the epidemic dynamics is the same, the migration dynamics should be different, especially if considered as part of a discrete randomized model approach (cf. [13, 14]).

In the paper we start with consideration of the simplest network of only two interacting epidemic SIR centra and study in detail the migration processes and their influence on the population dynamics. Moreover, our interest in the model is motivated by the fact that it serves as a hydrodynamic approximation of a natural Markov process describing the stochastic dynamics of the system (cf. [15]). This topic will be explored more fully in a subsequent paper.

To examine the migration model we first consider here the case when epidemic parameters are temporally switched off. The study of migration in isolation provides a simple tractable model and allows us to specify the parameters in a consistent way. Equally important, this analysis reveals that many models used in the literature (see eg [1, 16]) are unstable in the limit of vanishing infection. Other ones (see eg [17, 18]) remain stable but lead to non-realistic results.

Note that even an isolated SIR model cannot be integrated explicitly, therefore a suitable approximation is required to avoid numerical integration and to obtain practical formulas for outbreak time, fade-out time and other parameters. In our previous works [11, 12, 14] the so-called small initial contagion (SIC) approximation was proposed, based on the assumption that an outbreak in every population center is caused by relatively small number of initially infectives. This approximation is appropriate when the model is applied to strongly populated centra like urban centra (i.e. in the situation when the reaction-diffusion model is not accurate).

In the paper we also show how the model can be generalized on the general network of epidemic centra (see Section 7). As an example a characteristic equation for the travelling wave in a chain of the population centers is derived and its numerical solution is plotted and analyzed.

## 2 Governing equations

Consider two populated nodes, 1 and 2, with populations  $N_1$  and  $N_2$ , respectively. Let  $S_n(t)$ ,  $I_n(t)$ ,  $R_n(t)$  be the numbers of host susceptibles, infectives and removed, respectively, in node  $n$  at time  $t$ . Let  $S_{mn}(t)$ ,  $I_{mn}(t)$ ,  $R_{mn}(t)$  be numbers of guest susceptibles, infectives and removed, respectively, in node  $n$  migrated from node  $m$  at time  $t$ . Removed populations  $R_n$ ,  $R_{nm}$  do not affect dynamics of all others in the framework of the standard SIR model, and we omit them from consideration here. Then, two SIR centers (nodes) interacting due to the migration of individuals between them are described by the following model: the dynamics of hosts in node  $n$  obeys the ODEs

$$\dot{S}_n = -\beta_n S_n (I_n + I_{mn}) - \dot{S}_{n \rightarrow m} + \dot{S}_{n \leftarrow m} \quad (1)$$

$$\dot{I}_n = \beta_n S_n (I_n + I_{mn}) - \alpha_n I_n - \dot{I}_{n \rightarrow m} + \dot{I}_{n \leftarrow m} \quad (2)$$

where  $n = 1, 2$ ,  $m = 2, 1$ ; and dot denotes the time derivative. Here the term  $\beta_n S_n (I_n + I_{mn})$  appears due to infectives  $I_{mn}$  migrated from node  $m$  and contributing to the total disease transmission process. Terms  $\dot{S}_{n \rightarrow m}$  and  $\dot{I}_{n \rightarrow m}$  describe migration fluxes (rates) from node  $n$  to node  $m$  for susceptibles and infectives, respectively. Terms  $\dot{S}_{n \leftarrow m}$  and  $\dot{I}_{n \leftarrow m}$  describe return migration fluxes (rates) to node  $n$  for guest individuals in node  $m$ . We specify these below.

The dynamics of guests in node  $n$  temporally arriving from node  $m$  can be described by analogous ODEs

$$\dot{S}_{mn} = -\beta_n S_{mn} (I_n + I_{mn}) + \dot{S}_{m \rightarrow n} - \dot{S}_{m \leftarrow n} \quad (3)$$

$$\dot{I}_{mn} = \beta_n S_{mn} (I_n + I_{mn}) - \alpha_n I_{mn} + \dot{I}_{m \rightarrow n} - \dot{I}_{m \leftarrow n} \quad (4)$$

We assume the migration rate is proportional to the population size in the node from which they emigrate. So, we approximate the fluxes as

$$\begin{aligned} \dot{S}_{n \rightarrow m} &= \gamma_{nm}^S S_n, & \dot{I}_{n \rightarrow m} &= \gamma_{nm}^I I_n, \\ \dot{S}_{n \leftarrow m} &= \delta_{nm}^S S_{nm}, & \dot{I}_{n \leftarrow m} &= \delta_{nm}^I I_{nm} \end{aligned} \quad (5)$$

where  $\gamma$ 's and  $\delta$ 's are the forward and backward migration coefficients, respectively.

Our interest in the dynamical equations presented above is motivated by the fact that they serve as a hydrodynamic approximation of a Markov process model. In this context,  $\gamma$ 's can be associated with the transition rate for a host individual to migrate to another node in a unit of time, and  $\delta$ 's—with the transition rate for a guest individual to return to the host node.

Clearly, average return rates should be higher:  $\gamma_{nm}^S < \delta_{nm}^S$ ,  $\gamma_{nm}^I < \delta_{nm}^I$ , otherwise an individual would spend most of the time out of the home center.

Substituting (5) into (1)–(2) and (3)–(4) yields a closed system of ODEs: for the hosts in node  $n$

$$\dot{S}_n = -\beta_n S_n (I_n + I_{mn}) - \gamma_{nm}^S S_n + \delta_{nm}^S S_{nm} \quad (6)$$

$$\dot{I}_n = \beta_n S_n (I_n + I_{mn}) - \alpha_n I_n - \gamma_{nm}^I I_n + \delta_{nm}^I I_{nm} \quad (7)$$

and for the guests migrated from node  $m$  into node  $n$

$$\dot{S}_{mn} = -\beta_n S_{mn}(I_n + I_{mn}) + \gamma_{mn}^S S_m - \delta_{mn}^S S_{mn} \quad (8)$$

$$\dot{I}_{mn} = \beta_n S_{mn}(I_n + I_{mn}) - \alpha_n I_{mn} + \gamma_{mn}^I I_m - \delta_{mn}^I I_{mn}. \quad (9)$$

Evidently, the dynamics of hosts and guests are different.

Typical initial conditions for epidemiological problem describe a number of infectives, say  $I_{01}$ , that appeared at  $t = 0$  in node 1 only:

$$\begin{aligned} I_1(0) &= I_{01}, & I_2(0) &= 0, \\ S_1(0) &= N_1 - S_{12}(0) - I_{01}, & S_2(0) &= N_2 - S_{21}(0), \\ I_{12}(0) &= 0, & I_{21}(0) &= 0, \\ S_{12}(0) &= \frac{\gamma_{12}^S}{\gamma_{12}^S + \delta_{12}^S} N_1, & S_{21}(0) &= \frac{\gamma_{21}^S}{\gamma_{21}^S + \delta_{21}^S} N_2. \end{aligned} \quad (10)$$

The choice for values for  $S_{12}(0)$  and  $S_{21}(0)$  will be explained below in Section 3 by considering the migration processes before the epidemic outbreak starts.

### 3 Pure migration

Consider migration of susceptibles before the epidemic starts in the network. Setting  $I_1, I_{12}, I_2, I_{21} = 0$  we obtain two decoupled systems of ODEs for  $S_1, S_{12}$  and for  $S_2, S_{21}$  describing the pure migration processes in the absence of an outbreak. Say, for the pair  $S_1, S_{12}$  we have

$$\dot{S}_1 = -\gamma_{12}^S S_1 + \delta_{12}^S S_{12} \quad (11)$$

$$\dot{S}_{12} = \gamma_{12}^S S_1 - \delta_{12}^S S_{12}. \quad (12)$$

Let migration start at  $t = 0$  with the initial conditions  $S_1(0) = N_1, S_{12}(0) = 0$ . The solution to such an initial value problem is

$$S_{12} = N_1 g_{12}^S(t), \quad S_1 = N_1 - S_{12} \quad (13)$$

where

$$g_{12}^S(t) = \frac{\gamma_{12}^S}{\gamma_{12}^S + \delta_{12}^S} \left[ 1 - e^{-(\gamma_{12}^S + \delta_{12}^S)t} \right], \quad t \geq 0 \quad (14)$$

is the response function (see below). Similar formulas are valid for the second pair:  $S_2, S_{21}$ . Thus, the number of migrants exponentially tends to some limiting values

$$\lim_{t \rightarrow \infty} S_{12} = \frac{\gamma_{12}^S}{\gamma_{12}^S + \delta_{12}^S} N_1, \quad \lim_{t \rightarrow \infty} S_{21} = \frac{\gamma_{21}^S}{\gamma_{21}^S + \delta_{21}^S} N_2. \quad (15)$$

These limits represent the dynamic equilibrium of migration processes in the absence of the outbreak. At the equilibrium, the forward and backward migrations fluxes compensate each other:  $\dot{S}_{1 \rightarrow 2} = \dot{S}_{1 \leftarrow 2}$ . So, in virtue of (5),  $\gamma_{12}^S S_1 = \delta_{12}^S S_{12}$ . Substituting  $S_1 = N_1 - S_{12}$  and resolving with

respect to  $S_{12}$  yields (15). We take the equilibrium values from (15) as the initial conditions for the outbreak problem, that is reflected in (10).

The total populations in any node  $S_1^\Sigma = S_1 + S_{21}$  and  $S_2^\Sigma = S_2 + S_{12}$  are described as

$$\begin{aligned} S_1^\Sigma(t) &= N_1 - N_1 g_{12}(t) + N_2 g_{21}(t) \\ S_2^\Sigma(t) &= N_2 - N_2 g_{21}(t) + N_1 g_{12}(t). \end{aligned}$$

They can be non-monotonic for some choice of parameters. Next,  $S_{1,2}^\Sigma$  asymptotically converges to

$$\begin{aligned} S_1^\Sigma(+\infty) &= N_1 - N_1 \frac{\gamma_{12}^S}{\gamma_{12}^S + \delta_{12}^S} + N_2 \frac{\gamma_{21}^S}{\gamma_{21}^S + \delta_{21}^S} \\ S_2^\Sigma(+\infty) &= N_2 - N_2 \frac{\gamma_{21}^S}{\gamma_{21}^S + \delta_{21}^S} + N_1 \frac{\gamma_{12}^S}{\gamma_{12}^S + \delta_{12}^S}. \end{aligned}$$

If both centra are identical then their total population remains constant.

The migration dynamics described by this model seems reasonable. The migration process resembles a diffusion process in physics, in which the concentration tends monotonically to an equilibrium.

Note that if  $\gamma_{12}^S \ll \delta_{12}^S$  then  $S_{12}(t) \ll N_1, \forall t$ , i.e. only a small share of the population from of node 1 is currently in node 2 (and vice verse: if  $\gamma_{21}^S \ll \delta_{21}^S$  then  $S_{21}(t) \ll N_2, \forall t$ ), which is appropriate for large population centra. So, in this approximation  $S_{mn} \lesssim (\gamma_{mn}^S / \delta_{mn}^S) S_m$ .

To understand why function (14) can be associated with a response function, consider a model for which the number of susceptibles can vary even in the absence of migration due to other reasons (e.g., birth and death). Let  $\dot{N}_1$  be the rate of incoming ( $\dot{N}_1 > 0$ ) or outgoing ( $\dot{N}_1 < 0$ ) individuals, i.e. the external source in the equations

$$\begin{aligned} \dot{S}_1 &= -\gamma_{12}^S S_1 + \delta_{12}^S S_{12} + \dot{N}_1 \\ \dot{S}_{12} &= \gamma_{12}^S S_1 - \delta_{12}^S S_{12} \end{aligned} \tag{16}$$

with initial conditions  $S_1(0) = N_{01}$ ,  $S_{12}(0) = 0$ . Integrating the second equation in view of relation  $S_1 = N_1 - S_{12}$  yields:

$$S_{12}(t) = \int_0^t \gamma_{12}^S \exp \{ -(\gamma_{12}^S + \delta_{12}^S)(t - t') \} N_1(t') dt' \equiv \dot{g}_{12}^S(t) * N_1(t)$$

where the asterisk denotes the convolution,  $\dot{g}_{12}^S(t)$  is the derivative of function (14): recall that  $\dot{g}_{12}^S * H(t) = g_{12}^S$  where  $H(t)$  is the unit-step Heaviside function. So,  $S_{12} = \dot{g}_{12}^S(t) * N_1(t)$  is the response in the number of guests in node 2 on the population variation in node 1.

## 4 Comparison with earlier models

The most epidemic network models deal with the total number of infectives:  $I_n^\Sigma = I_n + I_{mn}$ , and susceptibles  $S_n^\Sigma = S_n + S_{mn}$  in node  $n$ . To compare these models take the sum of Eqs. (6) and (7)

and obtain the equations

$$\begin{aligned}\dot{S}_n^\Sigma &= -\beta_n S_n^\Sigma I_n^\Sigma - \gamma_{nm}^S S_n^\Sigma + \gamma_{mn}^S S_m^\Sigma - (\delta_{mn}^S - \gamma_{mn}^S) S_{mn} + (\delta_{nm}^S - \gamma_{nm}^S) S_{nm} \\ \dot{I}_n^\Sigma &= \beta_n S_n^\Sigma I_n^\Sigma - \alpha_n I_n^\Sigma - \gamma_{nm}^I I_n^\Sigma + \gamma_{mn}^I I_m^\Sigma - (\delta_{mn}^I - \gamma_{mn}^I) I_{mn} + (\delta_{nm}^I - \gamma_{nm}^I) I_{nm}.\end{aligned}$$

Thus, we cannot obtain equations for total numbers of species only: they become coupled with the equations for guest individuals. Even when the number of guests is relatively small  $S_{mn} \ll S_n$ ,  $I_{mn} \ll I_n$ , and the approximation  $I_n^\Sigma \approx I_n$ ,  $S_n^\Sigma \approx S_n$  holds, we cannot neglect terms with  $\delta$ 's because  $S_{mn} \ll S_n$ ,  $I_{mn} \ll I_n$  are not always can be valid. In fact, the terms with  $\gamma$ 's and  $\delta$ 's may be of the same order. This complicates the model but makes it more realistic.

Many authors simply insert terms proportional to the relevant population size in neighbouring nodes to provide coupling between SIR centra:

$$\dot{S}_n = -\beta_n S_n I_n + \chi_{mn}^S S_m \quad (17)$$

$$\dot{I}_n = \beta_n S_n I_n - \alpha_n I_n + \chi_{mn}^I I_m \quad (18)$$

where  $\chi_{mn}^{S,I} \geq 0$  are coupling coefficients (cf. [1, 16]). In the case of pure migration between two centra ( $\alpha_n = \beta_n = 0$ ,  $I_n = 0$ ) they are reduced to

$$\dot{S}_1 = \chi_{12}^S S_2, \quad \dot{S}_2 = \chi_{21}^S S_1. \quad (19)$$

Note that this model does not guarantee preservation of the total population size because the sum  $S_1 + S_2$  is variable

$$\dot{S}_1 + \dot{S}_2 = \chi_{12}^S S_2 + \chi_{21}^S S_1,$$

which is unrealistic. By eliminating one variable we see that the system has unstable dynamics

$$\ddot{S}_1 = \chi_{12}^S \chi_{21}^S S_1 \implies S_1 = A e^{\chi t} + B e^{-\chi t}, \quad \chi = \sqrt{\chi_{12}^S \chi_{21}^S} > 0,$$

i.e., a growing particular solution. Thus, the traditional approach does not describe the migration between centra properly. Although this instability can potentially be hidden in the background of the outbreak and not be observable in certain epidemic model scenarios.

Nevertheless the model can be easily corrected by introducing inverse fluxes (cf. [17, 18])

$$\dot{S}_n = -\beta_n S_n I_n + \chi_{mn}^S S_m - \chi_{nm}^S S_n \quad (20)$$

$$\dot{I}_n = \beta_n S_n I_n - \alpha_n I_n + \chi_{mn}^I I_m - \chi_{nm}^I I_n. \quad (21)$$

Then for a pure migration model we have

$$\dot{S}_1 = -\chi_{21}^S S_1 + \chi_{12}^S S_2, \quad \dot{S}_2 = \chi_{21}^S S_1 - \chi_{12}^S S_2 \quad (22)$$

implying  $S_1 + S_2 = \text{const.}$  The solutions of ODEs (22) with initial conditions  $S_1(0) = N_1$ ,  $S_2(0) = N_2$  demonstrate exponential, diffusion-like behaviour of each node population

$$\begin{aligned}S_1 &= \frac{\chi_{mn}^S (N_1 + N_2)}{\chi_{mn}^S + \chi_{nm}^S} + \frac{\chi_{nm}^S N_1 - \chi_{mn}^S N_2}{\chi_{mn}^S + \chi_{nm}^S} \exp [-(\chi_{mn}^S + \chi_{nm}^S) t] \\ S_2 &= \frac{\chi_{nm}^S (N_1 + N_2)}{\chi_{mn}^S + \chi_{nm}^S} + \frac{\chi_{mn}^S N_2 - \chi_{nm}^S N_1}{\chi_{mn}^S + \chi_{nm}^S} \exp [-(\chi_{mn}^S + \chi_{nm}^S) t].\end{aligned}$$

In the case  $\chi_{mn}^S = \chi_{nm}^S$  both solutions tend to  $S_1(+\infty) = S_2(+\infty) = \frac{1}{2}(N_1 + N_2)$ , i.e. their populations become equal (fully mixed). Thus the dynamics of the corrected model seems to be more realistic but nevertheless does not satisfy an intuitive interpretation of the equilibrium of the migration process.

In [12], in order to obtain more realistic migration dynamics, different flux terms are added to equations (6)–(7) in the form of convolutions (transition terms)

$$S_{n \rightarrow m} = \dot{g}_{nm}^S * S_n, \quad I_{n \rightarrow m} = \dot{g}_{nm}^I * I_n$$

where  $g$ 's are the relevant response functions. Then, the dynamics is described by integro-differential equations

$$\dot{S}_n = -\beta_n S_n I_n - \frac{d}{dt}(\dot{g}_{nm}^S * S_n) + \frac{d}{dt}(\dot{g}_{mn}^S * S_m) \quad (23)$$

$$\dot{I}_n = \beta_n S_n I_n - \alpha_n I_n - \frac{d}{dt}(\dot{g}_{nm}^I * I_n) + \frac{d}{dt}(\dot{g}_{mn}^I * I_m). \quad (24)$$

A natural choice for the response functions is the exponential form

$$g_{mn}^{I,S}(t) = \varepsilon_{mn}^{I,S} \left[ 1 - e^{-t/\tau_{mn}^{I,S}} \right] \quad (25)$$

where  $\tau$ 's are the characteristic migration times,  $\varepsilon$ 's are coupling parameters,  $t \geq 0$ . The form of these response functions is the same as in (14) obtained solving the initial value problem, see Section 3

Note that for a response function in the form of (25), the integro-differential equations (23)–(24) can be reduced to ODEs. We introduce additional variables  $S_{nm} = \dot{g}_{nm}^S * S_n$ ,  $I_{nm} = \dot{g}_{nm}^I * I_n$  which aim to capture the number of guests in node  $m$  coming from node  $n$ , in agreement with notations used in the present work. They obey the following ODEs

$$\dot{S}_{nm} + \frac{1}{\tau_{nm}^S} S_{nm} = \frac{\varepsilon_{nm}^S}{\tau_{nm}^S} S_n, \quad \dot{I}_{nm} + \frac{1}{\tau_{nm}^I} I_{nm} = \frac{\varepsilon_{nm}^I}{\tau_{nm}^I} I_n \quad (26)$$

that can be easily checked. Then ODEs

$$\dot{S}_n = -\beta_n S_n I_n - \dot{S}_{nm} + \dot{S}_{mn} \quad (27)$$

$$\dot{I}_n = \beta_n S_n I_n - \alpha_n I_n - \dot{I}_{nm} + \dot{I}_{mn} \quad (28)$$

together with ODEs (26) form a closed system of equations for  $n = 1, 2$  and  $m = 2, 1$ .

For a pure migration model (neglecting the outbreak dynamics) we obtain the following ODEs

$$\begin{aligned} \dot{S}_1 &= -\dot{S}_{12} + \dot{S}_{21}, & \dot{S}_{12} + S_{12}/\tau_{12}^S &= \varepsilon_{12}^S S_1 \\ \dot{S}_2 &= \dot{S}_{12} - \dot{S}_{21}, & \dot{S}_{21} + S_{21}/\tau_{21}^S &= \varepsilon_{21}^S S_2 \end{aligned} \quad (29)$$

with initial conditions  $S_1(0) = N_1$ ,  $S_2(0) = N_2$ ,  $S_{12}(0) = S_{21}(0) = 0$ .

Taking the sum of the two left equations we see that the total population is preserved:  $S_1 + S_2 = \text{const} = N_1 + N_2$ .

In the case of identical migration parameters for the both nodes:  $\tau_{12}^S = \tau_{21}^S = \tau$ ,  $\varepsilon_{12}^S = \varepsilon_{21}^S = \varepsilon$  the number of migrants in node 2 is described as in (13)–(14):

$$S_{12} = N_1 \frac{\varepsilon}{1 + 2\varepsilon} \left( 1 - \exp \left\{ -\frac{1 + 2\varepsilon}{\tau} t \right\} \right).$$

In the general case the solution can be represented via two exponential functions with different characteristic times  $\tau_1$  and  $\tau_2$  and not necessarily monotonic (which is quite unrealistic). Nevertheless, neglecting backward migration from node 2 to node 1 by setting  $S_{21} = 0$ , i.e. solving equations  $\dot{S}_1 = -\dot{S}_{12}$ ,  $\dot{S}_{12} + S_{12}/\tau_{12}^S = \varepsilon_{12}^S S_1$ , yields exactly the solution (13)–(14):

$$S_{12} = N_1 g_{12}^S = N_1 \varepsilon_{12}^S \left[ 1 - e^{-t/\tau_{12}^S} \right], \quad S_1 = N_1 - S_{12}.$$

Summing up, we conclude that the model proposed in the present work behaves appropriately: at first populations increase exponentially, then they tend monotonically to their final values, say  $S_1(+\infty) = N_1 - \varepsilon_{mn}^S N_1$ . Other useful approximations will be applied in specific situations.

Next we compare the response function (25) defined in [11, 12] and the response function (14), and express the basic migration parameters such as the migration characteristic time  $\tau_{12}^S$  and the coupling coefficient  $\varepsilon_{12}^S$  via the migration parameters  $\gamma_{12}^S$  and  $\delta_{12}^S$  introduced here:

$$\tau_{12}^S = \frac{1}{\gamma_{12}^S + \delta_{12}^S}, \quad \varepsilon_{12}^S = \frac{\gamma_{12}^S}{\gamma_{12}^S + \delta_{12}^S} \quad (30)$$

The inverse relations are

$$\gamma_{12}^S = \frac{\varepsilon_{12}^S}{\tau_{12}^S}, \quad \delta_{12}^S = \frac{1 - \varepsilon_{12}^S}{\tau_{12}^S}.$$

Coefficient  $\varepsilon_{12}^S$  represents a share of the population from node 1 migrated to node 2 at dynamical equilibrium or a share of time the individuals from node 1 spend in node 2 on average. In the case of small coupling, the estimation of the order of different terms is very useful.

Analogous response functions can be defined for all other population classes, they determine the dynamics due to pure migration when the disease transmission and removal is disregarded by setting  $\alpha$ 's and  $\beta$ 's to zero. The response function for the migration of susceptibles and infectives

$$g_{12}^{S,I}(t) = \varepsilon_{12}^{S,I} \left[ 1 - e^{-t/\tau_{12}^{S,I}} \right], \quad \tau_{12}^{S,I} = \frac{1}{\gamma_{12}^{S,I} + \delta_{12}^{S,I}}, \quad \varepsilon_{12}^{S,I} = \frac{\gamma_{12}^{S,I}}{\gamma_{12}^{S,I} + \delta_{12}^{S,I}} \quad (31)$$

will be used intensively below.

Examples of numerical solutions to the initial value problems (6)–(9)–(10) are shown in Figure 1.

## 5 Small initial contagion (SIC) approximation

In many situations the number of external infectives triggering an epidemic outbreak in a given center is small compared to the number of infectives occurring during the developed outbreak. If



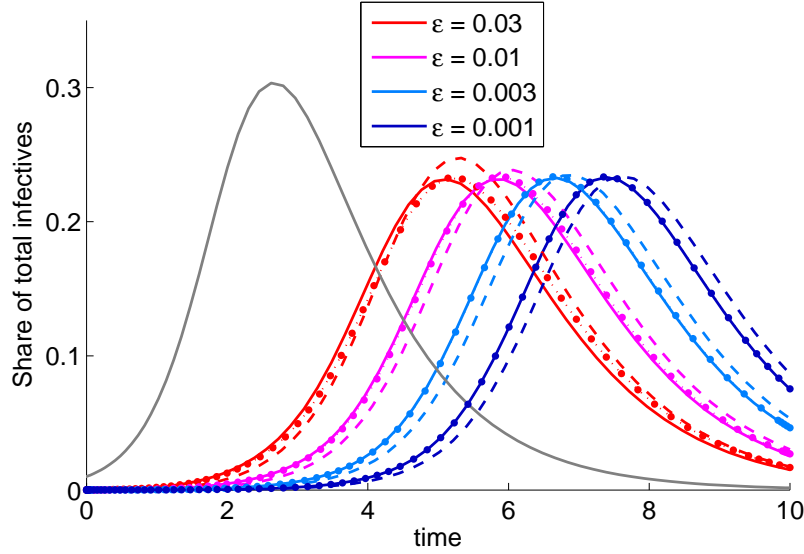


Figure 1: Dynamics of the total number of infectives  $I_2^\Sigma \equiv I_2 + I_{12}$  in the second node (divided by its population): (a) computed via the full equations (6)–(9) (colored solid line); by the SIC approximation (46)–(49) (dotted lines); assuming the absence of guest susceptibles before the outbreak (dashed lines). The curves are plotted for different values of the coupling coefficient  $\varepsilon_{12}^I \equiv \gamma_{12}^I/(\gamma_{12}^I + \delta_{12}^I)$  (indicated in the legend). Parameters:  $N_2/N_1 = 0.8$ ,  $\alpha_1 = \alpha_2 = 1$ ,  $\beta_1 = 3$ ,  $\beta_2 = 2.5$ ,  $\tau_{12}^{I,S} \equiv 1/(\gamma_{12}^{I,S} + \delta_{12}^{I,S}) = 3$ ,  $\varepsilon_{12}^S = \varepsilon_{21}^{I,S} = \varepsilon_{12}^I$ . The epidemic outbreak in the first node  $I_1^\Sigma \equiv I_1 + I_{21}$  (divided by its population) is indicated by a grey line.

this is the case, the model can be simplified in the framework of the small initial contagion (SIC) approximation introduced in [11, 12].

In the SIC approximation we can split the outbreak process in every node into two stages: (i) contamination and (ii) the developed outbreak. At the contamination stage, the number of infectives is relatively small whereas the total population consists mainly of susceptibles. Then on the r.h.s. of (6)–(9),  $S_1 \approx N_1$  and  $S_2 \approx N_2$ , the equations become linear and can be easily analyzed. At the second stage every node become non-sensitive to small migration processes and the dynamics can be well described by a standard SIR process.

In the SIC approximation, the initial number of infectives should be small that obviously can occur in a large population center. Thus the first conditions should be

$$N_n \gg 1, \quad \forall n. \quad (32)$$

Secondly, the coupling between nodes should be small, so that in the developed outbreak the flux of infective migrants remains small compared to the population of nodes to which those infectives travel. This implies that all  $\varepsilon$ 's (see (31)) are small:

$$\varepsilon_{12}^S = \frac{\gamma_{12}^S}{\gamma_{12}^S + \delta_{12}^S} \ll 1 \Leftrightarrow \gamma_{mn}^{I,S} \ll \delta_{mn}^{I,S}, \quad \forall m \neq n. \quad (33)$$

Next, consider a network of population centers. Let an initial number of infectives  $I_{0n}$  suddenly appear in one of the nodes, say in node  $n$ . Then  $I_{0n} \ll I_{bn}$  should hold where  $I_{bn} = \max \{I_n(t)\}$  is the number of infectives in the peak of the outbreak. But if infectives are arriving gradually into a node (which is almost always the case for many nodes in the network), then it is not their total number that is essential but some effective number of initial infectives  $I_{0n}^{\text{eff}}$ : earlier immigrated infectives have time to contaminate more local susceptibles than ones immigrated later. So, the effective number of initial infectives  $I_{0n}^{\text{eff}}$  should be a weighted integral of  $I_{nm}(t)$  (see below):  $I_{0n}^{\text{eff}} \ll I_{bn}$ .

Note if the basic reproduction number defined as

$$\rho_n = \frac{\beta_n N_n}{\alpha_n} \quad (34)$$

is not close to unity then  $I_{bn} \sim N_n$ . Thus, the additional and the most important condition to maintain the validity of the SIC approximation is

$$I_{0n}^{\text{eff}} \ll N_n \quad (35)$$

where  $I_{0n}^{\text{eff}}$  is defined below by (56) for the two-nodes network or by (66) for a general network.

If the reproduction number  $\rho_n$  only slightly exceeds unity, the number of infectives in the outbreak is estimated as follows (cf. [1])

$$I_{bn} \approx -\frac{N_n \ln(1 - I_{0n}/N_n)}{\rho_n} + \frac{N_n}{2} (\rho_n - 1)^2 + O[(\rho_n - 1)^3]. \quad (36)$$

So the relation  $I_{bn} \sim O(N_n)$  holds if (a)  $I_{0n} \sim N_n$  (in this case the outbreak is not evident as  $I_{bn} - I_{0n} \ll I_{0n}$ ) and (b) if

$$\rho_n - 1 \gg N_n^{-1/2}. \quad (37)$$

We conclude that the SIC approximation is reasonable for epidemic models under above condition (37).

In the SIC approximation, i.e. when conditions (32), (33), (35), (37) hold, migration fluxes are small. They cannot change dramatically the populations at all nodes. However, the fluxes of infectives from a node with an outbreak to a non-contaminated node are essential (as these fluxes trigger the outbreak in that node or another node at an early stage of outbreak development).

Consider the initial value problem (6)–(9)–(10) in the SIC approximation. As node 1 is contaminated first, it is not sensitive to the outbreak in node 2 which will develop after a certain delay.

To build asymptotic we assume that all coupling coefficients  $\varepsilon_{mn}^{S,I}$  are of the same order with respect to a small parameter  $\varepsilon$ :  $\varepsilon_{mn}^{S,I} \equiv \gamma_{mn}^{S,I}/(\gamma_{mn}^{S,I} + \delta_{mn}^{S,I}) = O(\varepsilon)$ . Also we assume that  $I_{mn} = O(\varepsilon)I_m$ ,  $S_{mn} = O(\varepsilon)S_m$ ,  $\delta_{mn}^{S,I} = O(1)\alpha_{m,n} = O(1)\beta_{m,n}N_{m,n}$ . Also at contamination stage  $I_2 < O(1)I_{21,12}$ ,  $S_2 \approx N_2 - S_{21}$ .

We rewrite equation (6)–(7) for host species in node 1 separating  $O(\varepsilon)$  terms and enclosing them in curly brackets

$$\begin{aligned} \dot{S}_1 &= -\beta_1 S_1 I_1 && + \{-\beta_1 S_1 I_{21} - \gamma_{12}^S S_1 + \delta_{12}^S S_{12}\} \\ \dot{I}_1 &= (\beta_1 S_1 - \alpha_1) I_1 && + \{\beta_1 S_1 I_{21} - \gamma_{12}^I I_1 + \delta_{12}^I I_{12}\}. \end{aligned}$$

Neglecting terms in curly brackets we see that outbreak in node 1 can be described by standard SIR model for an isolated node:

$$\dot{S}_1 = -\beta_1 S_1 I_1 \quad (38)$$

$$\dot{I}_1 = \beta_1 S_1 I_1 - \alpha_1 I_1. \quad (39)$$

Now we rewrite equation (6)–(7) for host species in node 2

$$\dot{S}_2 = -\beta_2 S_2 (I_2 + I_{12}) + \{-\gamma_{21}^S S_2 + \delta_{21}^S S_{21}\} \quad (40)$$

$$\dot{I}_2 = (\beta_2 S_2 - \alpha_2) I_2 + [\beta_2 S_2 I_{12}] + [\delta_{21}^I I_{21}] + \{-\gamma_{21}^I I_2\}. \quad (41)$$

Here the term remaining always small and to be neglected is enclosed in curly brackets. Small terms which can prevail at the stage of contamination when  $I_2$  is small are enclosed in square brackets. They are coupling terms and represent two fluxes:  $\mu_1(t) = \beta_2 S_2 I_{12}$  and  $\mu_2(t) = \delta_{21}^I I_{21}$ . Flux  $\mu_1$  is due to the infected individuals belonging to node 1 and currently migrated to node 2 contaminating susceptibles there. Flux  $\mu_2$  is due to susceptible individuals migrated to node 1 from node 2, contaminated there and returning as infectives their host node.

Rewrite equation (9) for  $I_{12}$ :

$$\dot{I}_{12} = -(\alpha_2 + \delta_{12}^I) I_{12} + \gamma_{12}^I I_1 + \{\beta_2 S_{12} (I_2 + I_{12})\}. \quad (42)$$

Terms in curly brackets are small and can be neglected.

Now we rewrite analogous equation for  $I_{21}$

$$\dot{I}_{21} = -(\alpha_1 + \delta_{21}^I) I_{21} + [\beta_1 S_{21} I_1] + \{\gamma_{21}^I I_2 + \beta_1 S_{21} I_{21}\}. \quad (43)$$

We can neglect terms in curly brackets but essential term in the square brackets should remain.

The value of  $S_{21}(t)$  initially equals  $\varepsilon_{21}^S = \gamma_{21}^S / (\gamma_{21}^S + \delta_{21}^S)$  but can vary during contamination stage. Its varying is described by equation (8)

$$\dot{S}_{21} = (-\beta_1 I_1 - \delta_{21}^S) S_{21} + \gamma_{21}^S S_2 + \{-\beta_1 S_{21} I_{21}\} \quad (44)$$

It can vary noticeably during contamination stage for node 2.

At the initial stage we can approximate  $S_2 \approx N_2 - S_{21}$

$$\dot{S}_{21} + (\beta_1 I_1(t) + \delta_{21}^S) S_{21} = \gamma_{21}^S (N_2 - S_{21})$$

or

$$\dot{S}_{21} + (\beta_1 I_1(t) + (\delta_{21}^S + \gamma_{21}^S)) S_{21} = \gamma_{21}^S N_2. \quad (45)$$

Re-writing (38) in the form  $\beta_1 I_1 = -\dot{S}_1 / S_1$  and also utilizing (30) we can write (45) as

$$\dot{S}_{21} + \left( -\frac{\dot{S}_1}{S_1} + \frac{1}{\tau_{21}^S} \right) S_{21} = \frac{S_{21}(0)}{\tau_{21}^S}$$

where  $S_{21}(0) = \varepsilon_{21}^S N_2$ . When  $S_1 = \text{const}$  it has a steady-state solution  $S_{21} = S_{21}(0)$ . In the case of the outbreak the solution can be written in the quadrature from

$$S_{21}(t) = S_{21}(0) \left( 1 + \frac{1}{\tau_{21}^S} \int_0^t e^{t'/\tau_{21}^S} \frac{N_1 dt'}{S_1(t')} \right) \frac{S_1(t)}{N_1} e^{-t/\tau_{21}^S}.$$

Coupling with node 1 is essential in the SIC approximation at the initial stage only before the developed outbreak. At this stage we solve (41)–(44) neglecting terms in the curly brackets (then it becomes a linear inhomogeneous system of ODEs) approximating  $S_2 \approx N_2$ :

$$\dot{I}_2 - (\beta_2 N_2 - \alpha_2) I_2 = \beta_2 N_2 I_{12} + \delta_{21}^I I_{21} \quad (46)$$

$$\dot{I}_{12} + (\alpha_2 + \delta_{12}^I) I_{12} = \gamma_{12}^I I_1 \quad (47)$$

$$\dot{I}_{21} + (\alpha_1 + \delta_{21}^I - \beta_1 N_2 S_{21}) I_{21} = \beta_1 N_2 (S_{21} I_1) \quad (48)$$

$$\dot{S}_{21} + (\beta_1 I_1(t) + (\delta_{21}^S + \gamma_{21}^S)) S_{21} = \gamma_{21}^S N_2. \quad (49)$$

We re-write first three equations in the simplest form introducing new parameters

$$\dot{I}_2 - \lambda_2 I_2 = a_{12} I_{12} + a_{21} I_{21} \quad (50)$$

$$\dot{I}_{12} + \lambda_{12} I_{12} = b_{12} I_1 \quad (51)$$

$$\dot{I}_{21} + \lambda_{21} I_{21} = b_{21} (S_{21} I_1) \quad (52)$$

where  $\lambda_2 = \beta_2 N_2 - \alpha_2 = (\rho_2 - 1) \alpha_2$  is initial growth rate in node 2;  $\lambda_{12} = (\alpha_2 + \delta_{12}^I)$  and  $\lambda_{21} = (\alpha_1 + \delta_{21}^I - \beta_1 \varepsilon_{21}^S N_2)$  are initial decay rate of guest species  $I_{21}$  and  $I_{12}$ , respectively;  $a_{12} = \beta_2 N_2$ ,  $a_{21} = \delta_{21}^I$ ,  $b_{12} = \gamma_{12}^I$ ,  $b_{21} = \beta_1 N_2$ . Note in the SIC approximation should be  $\beta_1 \varepsilon_{21}^S N_2 \ll \alpha_1$ ,  $\delta_{21}^I$  therefore  $\lambda_{21} \approx \alpha_1 + \delta_{21}^I > 0$ .

Solving system (50)–(52) by the Laplace transform method we obtain

$$\begin{aligned} I_{12} &= b_{12} I_1 * e^{-\lambda_{12} t}, & I_{21} &= b_{21} I_1 * e^{-\lambda_{21} t} \\ I_2 &= C_{12}^{(1)} I_1 * e^{\lambda_2 t} + C_{21}^{(2)} (S_{21} I_1) * e^{\lambda_2 t} \\ &\quad - \frac{a_{12} b_{12}}{\lambda_2 + \lambda_{12}} I_1 * e^{-\lambda_{12} t} - \frac{a_{21} b_{21}}{\lambda_2 + \lambda_{21}} (S_{21} I_1) * e^{-\lambda_{21} t}; \\ C_{12}^{(1)} &= \frac{a_{12} b_{12}}{\lambda_2 + \lambda_{12}}, & C_{21}^{(2)} &= \frac{a_{21} b_{21}}{\lambda_2 + \lambda_{21}} \end{aligned}$$

where  $*$  denotes the convolution. At time  $t \gtrsim \lambda_2^{-1}$  only the growing terms for  $I_2$  are essential, and the simplified expression takes the form

$$I_2 \simeq C_{12}^{(1)} \int_0^t I_1(t') e^{\lambda_2(t-t')} dt' + C_{21}^{(2)} \int_0^t S_{21}(t') I_1(t') e^{\lambda_2(t-t')} dt' \quad (53)$$

where

$$C_{12}^{(1)} = \frac{\gamma_{12}^I \beta_2 N_2}{\beta_2 N_2 + \delta_{12}^I}, \quad C_{21}^{(2)} = \frac{\delta_{21}^I \beta_1}{\beta_2 N_2 - \alpha_2 + \alpha_1 + \delta_{21}^I}. \quad (54)$$

Constant  $C_{12}^{(1)} = O(\varepsilon)$  as it is proportional to  $\gamma_{12}^I$ . Constant  $C_{21}^{(2)}$  is not small but the integrand contains value  $S_{21}$  which is proportional to  $\gamma_{21}^S$ , i.e. also has order  $O(\varepsilon)$ .

As  $I_1(t)$  in the integrand describes an outbreak in node 1 which is a decaying function after reaching the maximal outbreak in the node, we see that contribution of it in integral (53) is negligible after time  $t_*$ :  $t_{b1} < t_*$ . Thus for  $t > t_*$  function  $I_2(t)$  grows exponentially as in the standard SIR model

$$\begin{aligned} I_2 &\simeq e^{\lambda_2 t} \int_0^{t_*} \left( C_{12}^{(1)} + C_{21}^{(2)} S_{21}(t') \right) I_1(t') e^{-\lambda_2 t'} dt' \\ &\approx e^{\lambda_2 t} \int_0^{+\infty} \left( C_{12}^{(1)} + C_{21}^{(2)} S_{21}(t') \right) I_1(t') e^{-\lambda_2 t'} dt' = I_{02}^{\text{eff}} e^{\lambda_2 t}. \end{aligned} \quad (55)$$

Thus, we have the following evaluation for the effective number of infectives in node 2:

$$I_{02}^{\text{eff}} \approx \int_0^{+\infty} \left[ C_{12}^{(1)} I_1(t) + C_{21}^{(2)} S_{21}(t) I_1(t) \right] e^{-\lambda_2 t} dt. \quad (56)$$

Calculation of integral (56) needs simple approximation of solutions for the standard SIR model. It will be considered in a separate work.

## 6 Outbreak time

Next, we evaluate the outbreak time  $t_{bn}$ , the time from the introduction of infection up until the peak of the outbreak, in every node in the framework of the SIC approximation. Let the initial growth in the node 1 be an exponential:

$$I_1 \approx I_{01} e^{\lambda_1 t} \quad (57)$$

where  $\lambda_1$  is the initial growth rate of infectives in node 1

$$\lambda_1 = \beta_1 S_1(0) - \alpha_1 \approx \beta_1 N_1 - \alpha_1 = \alpha_1 (\rho_1 - 1). \quad (58)$$

Subsequent behaviour in the first center can be approximated by the limiting solution  $i^{\text{lim}}(t; \rho)$  introduced and described in [11, 12]

$$I_1 = N_1 i^{\text{lim}}[\alpha_1(t - t_{b1}(I_{01})); \rho_1] \quad (59)$$

where  $i = I/N$  is the share of infectives in the node.

The outbreak time  $t_{b1}(I_{01})$  can be roughly approximated by [11, 12]

$$t_{b1} = \frac{1}{\lambda_1} \ln \frac{A_0 N_1}{I_{01}} \approx \frac{1}{\lambda_1} \ln \frac{\lambda_1 N_1}{\alpha_1 I_{01}}. \quad (60)$$

where  $A_0(\rho_1)$  is the parameter of the large negative time asymptotics of the limiting solution:

$$i^{\text{lim}} \rightarrow A_0 e^{\lambda_1(t - t_{b1})}, \quad t \rightarrow -\infty.$$

This shows the share of infectives at the instant of contamination that is required to trigger an outbreak under the assumption that the initial exponential growth continues up to the moment of the peak of the outbreak.

The dynamics of  $I_2$  is described by (53) at the initial stages before the developed outbreak: at the contamination stage when the migration of infectives from node 1 is essential and at the stage of exponential growth. At this stage (55) the coupling can be neglected and the dynamics is described by a limiting solution

$$I_2 = N_2 i^{\lim} [\alpha_2 (t - t_{b2}) ; \rho_2] \approx N_2 A_0 e^{\lambda_2 (t - t_{b2})}. \quad (61)$$

Comparing (55) and (61) we elaborate that

$$t_{b2} = \frac{1}{\lambda_2} \ln \frac{A_0 N_2}{I_{02}^{\text{eff}}} \approx \frac{1}{\lambda_2} \ln \frac{\lambda_2 N_2}{\alpha_2 I_{02}^{\text{eff}}}.$$

## 7 Epidemic spread in a 1D lattice of coupled SIR nodes

In the case of a general network of  $M$  interacting nodes Eqs. (6)–(7)–(8)–(9) should be slightly modified to account for all guests arriving at a given node  $n$ :

$$\dot{S}_n = -\beta_n S_n (I_n + \sum_{m \neq n} I_{mn}) - \sum_{m \neq n} \gamma_{nm}^S S_n + \sum_{m \neq n} \delta_{nm}^S S_{nm} \quad (62)$$

$$\dot{I}_n = \beta_n S_n (I_n + \sum_{m \neq n} I_{mn}) - \alpha_n I_n - \sum_{m \neq n} \gamma_{nm}^I I_n + \sum_{m \neq n} \delta_{nm}^I I_{nm} \quad (63)$$

$$\dot{S}_{mn} = -\beta_n S_{mn} (I_n + \sum_{m \neq n} I_{mn}) + \gamma_{mn}^S S_m - \sum_{m \neq n} \delta_{mn}^S S_{mn} \quad (64)$$

$$\dot{I}_{mn} = \beta_n S_{mn} (I_n + \sum_{m \neq n} I_{mn}) - \alpha_n I_{mn} + \gamma_{mn}^I I_m - \sum_{m \neq n} \delta_{mn}^I I_{mn}. \quad (65)$$

Interaction between nodes is determined by  $M \times M$  matrices  $\gamma_{mn}^{I,S}$ ,  $\delta_{mn}^{I,S}$ , and also matrices of guest populations  $S_{mn}$  and  $I_{mn}$ . All these matrices have zero diagonal elements, and they may also have zero elements if nodes  $m$  and  $n$  do not interact directly.

The effective number of initial infectives for the network in the SIC approximation can be calculated by the sum

$$I_{0n}^{\text{eff}} \approx \sum_{m \neq n} \int_0^{+\infty} [C_{mn}^{(1)} I_m(t) + C_{nm}^{(2)} S_{nm}(t) I_m(t)] e^{-\lambda_n t} dt \quad (66)$$

$$C_{mn}^{(1)} = \frac{\gamma_{mn}^I \beta_n N_n}{\beta_n N_n + \delta_{mn}^I}, \quad C_{nm}^{(2)} = \frac{\delta_{nm}^I \beta_m}{\beta_n N_n - \alpha_n + \alpha_m + \delta_{nm}^I}.$$

Consider, for example, an infinite 1D lattice of SIR centra where every node  $n$  interacts with its nearest neighbours  $m = n - 1$  and  $m = n + 1$ . For simplicity consider a network with identical

centra:  $\beta_n = \beta$ ,  $\alpha_n = \alpha$ ,  $N_n = N$  for  $\forall n$ . Also, let migration parameters be identical for every node and for every population class:  $\gamma_{mn}^{I,S} = \gamma$ ,  $\delta_{mn}^{I,S} = \delta$  for  $m = n \pm 1$  and  $\gamma_{mn}^{I,S} = 0$ ,  $\delta_{mn}^{I,S} = 0$  otherwise. Then we obtain a closed system of ODE

$$\dot{S}_n = -\beta S_n(I_n + I_{n-1n} + I_{n+1n}) - 2\gamma S_n + \delta S_{nn-1} + \delta S_{nn+1} \quad (67)$$

$$\dot{I}_n = \beta S_n(I_n + I_{n-1n} + I_{n+1n}) - \alpha I_n - 2\gamma I_n + \delta I_{nn-1} + \delta I_{nn+1} \quad (68)$$

taking into account Eqs. (8)–(9) with  $m = n \pm 1$

$$\dot{S}_{n\pm 1n} = -\beta S_{n\pm 1n}(I_n + I_{n-1n} + I_{n+1n}) + \gamma S_{n\pm 1} - \delta S_{n\pm 1n} \quad (69)$$

$$\dot{I}_{n\pm 1n} = \beta S_{n\pm 1n}(I_n + I_{n-1n} + I_{n+1n}) - \alpha I_{n\pm 1n} + \gamma I_{n\pm 1} - \delta I_{n\pm 1n}. \quad (70)$$

When parameters of nodes are identical we can introduce the universal dimensionless time  $t' = \alpha t$  and dimensionless migration parameters  $\gamma' = \gamma/\alpha$ ,  $\delta' = \delta/\alpha$ . Also define the shares of host and guest infectives  $i_n = I_n/N$ ,  $i_{mn} = I_{mn}/N$  and susceptibles  $s_n = S_n/N$ ,  $s_{mn} = S_{mn}/N$ . Then we can rewrite the equations in terms of dimensionless variables, omitting primes:

$$\dot{s}_n = -\rho s_n(i_n + i_{n-1n} + i_{n+1n}) - 2\gamma s_n + \delta s_{nn-1} + \delta s_{nn+1} \quad (71)$$

$$\dot{i}_n = \rho s_n(i_n + i_{n-1n} + i_{n+1n}) - i_n - 2\gamma i_n + \delta i_{nn-1} + \delta i_{nn+1} \quad (72)$$

$$\dot{s}_{n\pm 1n} = -\rho s_{n\pm 1n}(i_n + i_{n-1n} + i_{n+1n}) + \gamma s_{n\pm 1} - \delta s_{n\pm 1n} \quad (73)$$

$$\dot{i}_{n\pm 1n} = \rho s_{n\pm 1n}(i_n + i_{n-1n} + i_{n+1n}) - i_{n\pm 1n} + \gamma i_{n\pm 1} - \delta i_{n\pm 1n}. \quad (74)$$

We search for the travelling wave in the form

$$s_n(t) = s^{\text{tr}}(t - Tn), \quad i_n(t) = i^{\text{tr}}(t - Tn) \quad (75)$$

$$s_{n\pm 1n}(t) = s_{\pm}^{\text{tr}}(t - Tn), \quad i_{n\pm 1n}(t) = i_{\pm}^{\text{tr}}(t - Tn) \quad (76)$$

$$s_{nn\pm 1}(t) = s_{\mp}^{\text{tr}}(t - T(n \pm 1)), \quad i_{nn\pm 1}(t) = i_{\mp}^{\text{tr}}(t - T(n \pm 1)) \quad (77)$$

where  $T$  is the time lag between outbreaks in two neighbour nodes. Here  $i^{\text{tr}}(t)$ ,  $s^{\text{tr}}(t)$  are the shares of hosts in node  $n = 0$ ;  $i_-^{\text{tr}}(t)$ ,  $s_-^{\text{tr}}(t)$  are the shares of guests in node  $n = 0$  arrived from node  $n = -1$ ;  $i_+^{\text{tr}}(t)$ ,  $s_+^{\text{tr}}(t)$  are the shares of guests in node  $n = 0$  arrived from node  $n = +1$ ;  $i_-^{\text{tr}}(t + T)$ ,  $s_-^{\text{tr}}(t + T)$  are the shares of guests in node  $n = 1$  arrived from node  $n = 0$ ;  $i_+^{\text{tr}}(t - T)$ ,  $s_+^{\text{tr}}(t - T)$  are the shares of guests in node  $n = -1$  arrived from node  $n = 0$ .

Substituting (75)–(77) into (71)–(74) we obtain the system of ODEs

$$\dot{s}^{\text{tr}} = -\rho s(i^{\text{tr}} + i_-^{\text{tr}} + i_+^{\text{tr}}) - 2\gamma s^{\text{tr}} + \delta s_-^{\text{tr}}(t + T) + \delta s_+^{\text{tr}}(t - T) \quad (78)$$

$$\dot{i}^{\text{tr}} = \rho s(i^{\text{tr}} + i_-^{\text{tr}} + i_+^{\text{tr}}) - i^{\text{tr}} - 2\gamma i^{\text{tr}} + \delta i_-^{\text{tr}}(t + T) + \delta i_+^{\text{tr}}(t - T) \quad (79)$$

$$\dot{s}_{\pm}^{\text{tr}} = -\rho s_{\pm}^{\text{tr}}(i^{\text{tr}} + i_-^{\text{tr}} + i_+^{\text{tr}}) + \gamma s^{\text{tr}}(t \pm T) - \delta s_{\pm}^{\text{tr}} \quad (80)$$

$$\dot{i}_{\pm}^{\text{tr}} = \rho s_{\pm}^{\text{tr}}(i^{\text{tr}} + i_-^{\text{tr}} + i_+^{\text{tr}}) - i_{\pm}^{\text{tr}} + \gamma i^{\text{tr}}(t \pm T) - \delta i_{\pm}^{\text{tr}}. \quad (81)$$

A travelling wave should satisfy the initial conditions (dynamic equilibrium in the absence of outbreak):

$$s^{\text{tr}}(-\infty) = 1, \quad i^{\text{tr}}(-\infty) = 0, \quad s_{\pm}^{\text{tr}}(-\infty) = \bar{\varepsilon}, \quad i_{\pm}^{\text{tr}}(-\infty) = 0. \quad (82)$$

Here  $\bar{\varepsilon} = \gamma / (\gamma + \delta)$  is the share of guest susceptibles at equilibrium in the absence of an outbreak (see (15)), it will be used in the analysis of the influence of guest susceptibles before the outbreak and slightly simplifies the equations.

When  $t \rightarrow -\infty$  the travelling wave initially have exponential growth. We substitute solution in the form

$$s^{\text{tr}}(t) = 1 - \Delta s^{\text{tr}} e^{\lambda t}, i^{\text{tr}}(t) = i e^{\lambda t}, s_{\pm}^{\text{tr}}(t) = \bar{\varepsilon} - \Delta s_{\pm}^{\text{tr}} e^{\lambda t}, i_{\pm}^{\text{tr}}(t) = i_{\pm} e^{\lambda t}$$

into (78)–(81) and linearize the equations with respect to  $\Delta s^{\text{tr}}, i^{\text{tr}}, \Delta s_{\pm}^{\text{tr}}, i_{\pm}^{\text{tr}}$ .

The values  $i, i_-, i_+$  satisfy the following system of linear algebraic equations

$$\lambda i = \rho(i + i_- + i_+) - i - 2\gamma i + \delta i_- e^{\lambda T} + \delta i_+ e^{-\lambda T} \quad (83)$$

$$\lambda i_{\pm} = \rho \bar{\varepsilon}(i + i_- + i_+) - i_{\pm} + \gamma i e^{\pm \lambda T} - \delta i_{\pm} \quad (84)$$

which has the following characteristic equation

$$L = \lambda_0 - \lambda - 2\gamma + \frac{2\gamma\delta}{\lambda + 1 + \delta} + \frac{2\bar{\varepsilon}\rho^2}{\lambda + 1 + \delta - 2\bar{\varepsilon}\rho} + \frac{2(\gamma + \bar{\varepsilon}\delta) \cosh(\lambda T)}{\lambda + 1 + \delta - 2\bar{\varepsilon}\rho} + \frac{2\bar{\varepsilon}\gamma\delta \cosh(2\lambda T)}{(\lambda + 1 + \delta)(\lambda + 1 + \delta - 2\bar{\varepsilon}\rho)} = 0$$

where  $\lambda_0 = \rho - 1$  is the initial growth rate of the limiting solution in the dimensionless time  $t' = \alpha t$ .

In the case  $\bar{\varepsilon} = 0$  we have

$$L_{\bar{\varepsilon}=0} = \lambda_0 - \lambda - \frac{2\gamma(\lambda + 1)}{\lambda + 1 + \delta} + \frac{2\gamma(\lambda_0 + 1)}{\lambda + 1 + \delta} \cosh(\lambda T). \quad (85)$$

By analogy with [12] (Eq. (42) there) we express these formulas in terms of  $\gamma$  and  $\delta$

$$L_{[12]} = \lambda_0 - \lambda - \frac{2\lambda\gamma}{\lambda + \gamma + \delta} \cosh(\lambda T). \quad (86)$$

Last two formulas have some similarities but do not coincide exactly.

In accordance with the principle of linear spreading velocity (LSV) (cf. [19, 20, 21, 22, 12]) we solve the system  $L = 0, \partial L / \partial \lambda$  with respect to  $\lambda$  and  $T$ .

The results from numerical exercises are shown in Figure 2 with  $\lambda_0 T$  vs  $\lambda_0 \tau$  for different  $\varepsilon = \gamma / (\gamma + \delta)$  and  $\rho$  (solid color lines) where  $\lambda_0 = \rho - 1$  is the initial growth rate for an individual SIR node in the SIC approximation. Recall that in terms of dimensional parameters they are  $(\rho - 1)\alpha T$  and  $(\rho - 1)\frac{\alpha}{\gamma + \delta}$ , respectively. Here dashed color curves are plotted for the case  $\bar{\varepsilon} = 0$ , i.e. neglecting guest susceptibles before the outbreak. Also curves obtained in from Eq. (86) are plotted by black lines. We make the following observations:

1. Note that the functions  $\lambda_0 T(\lambda_0 \tau)$  depend on  $\rho$  but not to a large extent: the smaller coupling  $\varepsilon$  — the smaller dependence. More discrepancy is observed for small  $\tau$ .
2. The curves for  $\bar{\varepsilon} = 0$  are very close to those obtained in [12], especially for small  $\varepsilon$ .



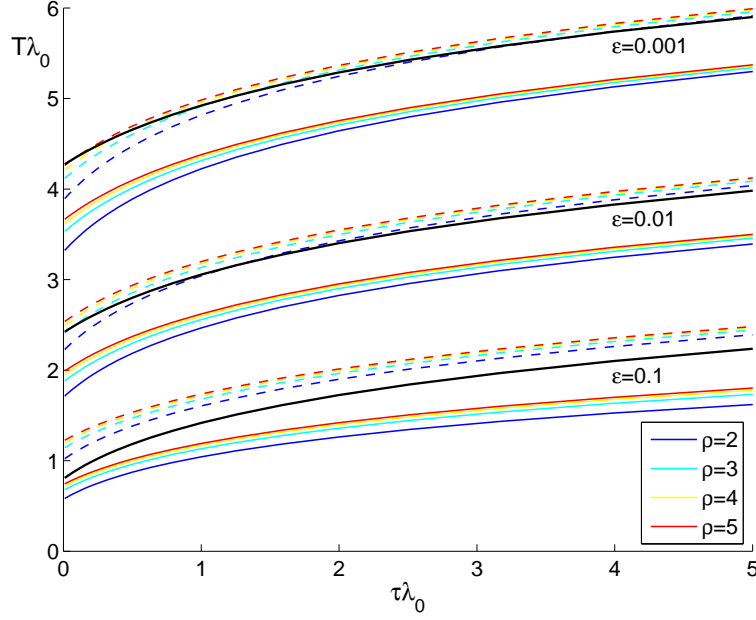


Figure 2: Color solid curves depict dependence of the dimensionless time lag (slowness) for traveling waves  $\lambda_0 T$  on the characteristic migration time  $\lambda_0 \tau$  for different  $\varepsilon \equiv \gamma/(\gamma+\delta)$  (indicated near the curves) and reproduction number  $\rho$  (indicated in the legend). Colored dashed curve depict the same dependencies in the case of an absence of guest susceptibles before the outbreak:  $\bar{\varepsilon} = 0$ . The black lines depict the similar curves taken from work [12]; they are independent of  $\rho$ .

3. Taking account of pre-outbreak guest susceptibles ( $\bar{\varepsilon} \neq 0$ ) noticeably shortens the time lag, i.e. it accelerates the propagation of the epidemic.

This indicates the importance of modelling guest populations separately. Guest susceptibles have much higher probability of returning to the host node than that for the simple migration process away from a home node. Correspondingly those susceptibles being contaminated have a relatively high probability of bringing back disease into their own host node, triggering an outbreak there, and continuing the propagation of the overall epidemic.

## 8 Conclusion

We explore analytically and numerically the SIR epidemic processes on a system of linked centra, and investigate of the importance of population structure on the developing dynamics of directly transmitted diseases. The deterministic model of the migration process between two population centra demonstrates the different rôle of susceptibles and infectives in the epidemic spread across the population as a whole.

The careful consideration of this simplified deterministic model allows us to derive the characteristic equation and hence to evaluate the speed of epidemic propagation via the chain of similar nodes. The model demonstrates that the epidemic speed is dependent on reproduction number  $\rho$

but not to a large extent, and this dependence declines to zero when the coupling vanishes. We also show that the appearance of pre-outbreak susceptibles accelerates the propagation of epidemic. The estimation of phenomenological parameters of the deterministic model  $\epsilon$  and  $\tau$  requires disease specific data. However, the study of pure migration (via questionnaire or transport data) can be related to parameters  $\gamma$  and  $\delta$  (cf. (31)). We note, however, that these models serve as a hydrodynamic approximation for a Markov process describing fluctuations in the discrete numbers of all types of individuals involved. In the framework of stochastic models  $\gamma$  and  $\delta$  are treated as the transition rates, or probabilities of a movements of a specific individual to a different center. A focus for future work will be to estimate the influence of random fluctuations on epidemic speed and discuss the more complicated situation of a network with several routes of introduction of contamination in any particular population centre.

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